

borers in subsistence cereal cultivation, initially in East Africa, by a push-pull intercropping strategy. The programme involves scientists from the International Centre of Insect Physiology and Ecology, Kenya (ICIPE), and the Kenya Agricultural Research Institute, in collaboration with IACR-Rothamsted and employs field sites near Kitale in northern Kenya and at the ICIPE Mbita Point Field Station on Lake Victoria. The programme is funded by the Gatsby Charitable Foundation as part of its strategy of financing collaborative projects between international research centres in Africa and advanced research centres in the UK.

Two main species of lepidopterous stem borers, one an indigenous Noctuid, *Busseola fusca* (Full.) and the other an introduced species of Pyralid, *Chilo partellus* Swinh., bore at the larval stage into the stems of sorghum and maize, causing complete destruction of the plant or drastic reduction in yield. Six key host plant compounds, including eugenol (4-allyl-2-methoxyphenol), have been identified by electrophysical studies at Rothamsted and shown to be attractive in behavioral studies in Kenya. Repellents from non-host plants, e.g., molasses grass, *Melinis minutiflora* Beauv., have been similarly identified and include  $\alpha$ -terpinolene. Following this understanding of volatile components employed by the pests in locating suitable hosts and avoiding non-hosts, a field control programme is being developed involving intercropping of maize and sorghum with other species selected for behavioural activity.

Striking results have been obtained against stem borer colonisation with certain intercropping regimes; for example, when the cereal crop was surrounded by a barrier of Napier grass, *Pennisetum purpureum* Schumacher., the adults laid eggs preferentially in the latter. However, the larvae failed to develop to adulthood, although at the same time, normal levels of parasitism were maintained.

With the non-host grass *M. minutiflora* as an intercrop, direct repulsion of the pests occurred, as was also found with a *Desmodium* species of nitrogen-fixing legume. In each case, the intercrop can be used as cattle feed, although a 'training period' may be necessary for the new forage to be acceptable to cattle. This strategy fits in well with small or medium-sized farms, i.e., up to 50 ha, which have an appropriate mix of cereal and cattle production or are in communities where trade in a surplus of either crop type can easily be managed. In addition to the direct reduction of stem borers through some of the intercropping programmes, improvements in parasitism have been observed with the intercrop of *M. minutiflora*.<sup>3</sup> The trap crop, *P. purpureum*, also acts as a windbreak, preventing lodging of maize.

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### Semiochemicals to Increase Parasitism in Aphid Pest Control

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Parasitic wasps or parasitoids are important biological control agents which have been used extensively in biological control and integrated pest management schemes in agriculture in many parts of the world. Some parasitoids are specific natural enemies of aphids and several species of these are produced commercially for use against aphid pests, principally on protected crops. A number of European species have been introduced into other regions of the world to help to control aphids on arable crops such as legumes and cereals. Aphid parasitoids have considerable potential as biological control agents but their efficiency is dependent upon their presence in the right place at the right time; their appearance in crops should be synchronized with colonising pest populations early in the season. Our understanding of parasitoid behaviour, particularly their responses to semiochemical cues during the host location and host recognition phases of the foraging process, is providing exciting opportunities for the manipulation of parasitoids in the field to enhance their impact on pest populations.<sup>1</sup> However, to develop realistic pest control strategies involving manipulation with

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semiochemicals, knowledge of parasitoid behaviour gleaned from laboratory studies must be combined with a sound understanding of their ecology.

Recent work by entomologists and chemical ecologists at IACR-Rothamsted, in collaboration with the University of Potenza in Italy, has demonstrated the role of plant volatiles in host location by female aphid parasitoids.<sup>1-3</sup> Parasitoid flight responses to semiochemical foraging cues were investigated in the laboratory using a wind tunnel. Females of the parasitoid *Aphidius ervi* Hal., whose principal host is the pea aphid *Acyrtosiphon pisum* (Harr.), responded strongly to odour from broad bean plants (*Vicia faba* L.) infested with host aphids but not to uninfested plants or to aphids alone. They also responded strongly to plants which had been infested with aphids but from which the aphids had recently been removed. The plant appeared to release volatiles, which acted as synomones, in response to aphid feeding damage. Such host-induced plant volatiles acting as host location synomones have previously been noted for parasitoids of caterpillars<sup>4</sup> and for predatory mites feeding on spider mites.<sup>5</sup> Interestingly, bean plants infested with a different aphid species, the black bean aphid *Aphis faba* Scop., which is not a host for *A. ervi*, were not attractive to the parasitoids. This suggests that the feeding action of different aphid species induces different changes in the volatiles released by the food plant. Further trials indicated that the host-induced volatiles were systematically released throughout the plant and their production was influenced by a combination of the number of aphids present and the period of infestation.

Plant volatiles were collected by air entrainment from above uninfested bean plants and plants infested by either pea aphids or black bean aphids. The flight responses of female *A. ervi* to these volatile extracts, placed on filter paper, were investigated in the wind tunnel. Volatiles entrained from host-infested plants elicited strong flight responses, whereas those from uninfested plants or plants infested with nonhost aphids did not. Further analysis of the entrained volatile extracts, using gas chromatography-mass spectrometry, revealed significant quantitative and qualitative differences amongst the three extracts. On the basis of these differences, several individual compounds are currently being tested for their attractiveness to female parasitoids. Such compounds could be developed to manipulate parasitoid populations in the field as part of 'push-pull' or stimulo-deterrent diversionary pest control strategies. Understanding the physiological and biochemical processes involved in the production of aphid-induced plant volatiles may open up the possibility of enhancing their production in crop plants through selective breeding or even molecular manipulation.

Other work at IACR-Rothamsted, in collaboration with colleagues at Imperial College (Silwood Park), has

revealed that female aphid parasitoids are also attracted to aphid sex pheromones.<sup>6</sup> In early field trials, simple Petri-dish traps baited with synthetic aphid sex pheromones, particularly the pheromone component (+)-(4aS,7S,7aR)-nepetalactone, caught large numbers of female parasitoids belonging to the genus *Praon*.<sup>7</sup> Subsequently, electrophysiology studies indicated that a wide range of aphid parasitoids had antennal receptors for aphid sex pheromone components, and several species flew to filter paper impregnated with pheromones in the wind tunnel. In recent field studies, aphid sex pheromone lures significantly increased rates of parasitism in pea aphid and cereal aphid populations on trap plants placed in field margins in autumn and in aphid populations in plots of winter wheat in summer. In addition to the generalist parasitoid *Praon volucre*, the cereal aphid specialist *Aphidius rhopalosiphii* and the pea aphid specialists *A. ervi* and *Aphidius eadyi* responded to the lures in these field trials.

Currently, a parasitoid manipulation strategy is being developed based on these parasitoid responses to synthetic aphid sex pheromones. The strategy aims to promote synchrony between parasitoids and their aphid hosts early in the season when the pests first colonise crop fields. This synchrony sometimes occurs naturally in crops such as cereals, enabling the parasitoids to reduce the initial aphid population growth rate to such an extent that other natural enemies can later prevent the pest from reaching economic damage thresholds.<sup>8</sup> We are attempting to concentrate overwintering parasitoids in vegetation strips along fields margins, designed and managed to provide hosts and winter shelter, by using aphid sex pheromone lures to attract them when they are dispersing from crop fields at the end of summer. This should ensure more rapid re-colonisation of crops the following spring and therefore better synchrony with invading aphids.

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## The Commercial Exploitation of Pheromones and other Semiochemicals

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### Introduction

It is now almost 40 years since the first insect pheromone was isolated and identified and many authors have referred over the years to their commercial potential. Much progress has been made during those years in terms of scientific and technological advances related to semiochemicals and in our understanding of pest behavioural ecology,<sup>1,2</sup> but few authors have questioned the ‘progress’ that has actually been made in terms of the commercial exploitation of pheromones and other semiochemicals; this paper reviews the extent to which the potential of these substances has been translated into commercial reality.

### The semiochemical industry today

Based on published data and unpublished information which has been made available to the author, semiochemical-based products are estimated to have world-wide sales in the US\$ 70–80 million range at the manufacturers’ level. This compares with a world-wide insecticide market of nearly US\$ 8 billion in 1995<sup>3</sup> so that it therefore constitutes less than 1% of that market. In terms of the biopesticide market (bacteria, viruses,

botanical insecticides, entomopathogenic nematodes and beneficial insects) on the other hand, semiochemicals constitute a much higher percentage (c. 30%) and probably are third in importance after bacterial and botanical products.<sup>4</sup> The industry has taken over 20 years to achieve its current size and this growth has been pioneered mostly by small to medium-sized enterprises (SMEs).

Semiochemical-based products have found markets all over the world, with no great concentration on any one continent. The producers of these products, however, are concentrated in the USA, Europe and Japan, and over 60% of the sales are achieved by about a dozen companies. The sale of traps and lures for monitoring insect pests accounts for nearly 40% of the semiochemical market, while the bulk of the remaining sales comes from mating disruption products for moth pests. Table 1 shows the geographic spread of the market by sales and pest species together with the names of the principal companies involved in the industry.

### Semiochemical-based products for insect pest monitoring

Pheromone-based monitoring systems provide one of the most reliable and effective survey methods for pest detection and quantification.<sup>5,6</sup> They have been used extensively in quarantine pest detection and in detecting movement of pest species into a crop. There have been difficulties in their use for quantitative measurements of insect populations but their role in optimising the timing of insecticide applications is growing in popularity and has led to substantial reductions in pesticide use. Although the market expectations for semiochemical-based products in insect monitoring were never very great, an estimate of their current global sales for this purpose at the manufacturers’ level comes to about US\$ 27 million. In many cases the market had to be generated from an almost non-existent base. These products have found their way into most situations where insects are a problem, including the major world crops cotton, rice, vegetables, fruit, forestry and protected horticultural crops, and also where pests attack food and fibre during their manufacture, storage and distribution. The regulatory hurdles for these products are not very significant given that they are used for ‘monitoring’ pests and not for ‘controlling’, ‘suppressing’ or in any way ‘mitigating’ their numbers. Such intentions for a product would immediately subject it to the regulatory processes relating to that intended use.

Monitoring systems are best viewed as diagnostic kits in terms of their market potential, their purpose for use and their regulatory treatment.<sup>7</sup> The growth in the use of semiochemical-based monitoring traps has been substantial over the last two decades and will continue in the future, given the ever-increasing concerns about pesticide residues in food, the need to reduce pesticide usage, and the food industry’s preoccupation with risk